

MISCELLANEOUS.

On the Morphology and Affinities of the Brachiopoda.

By H. LACAZE-DUTHIERS.

FEW animals are so widely diffused in the strata of the surface of the globe as the Brachiopoda, and few consequently are so frequently in the hands of naturalists; nevertheless, although they are represented by many species living in our seas, their zoological relations and their general plan of organization are by no means agreed upon.

Placed in the first instance among the Acephala, side by side with the Lamellibranchiata, they now justly form a distinct division; but the relationships of this division are far from being the same in the eyes of all zoologists. Thus, to dwell only upon the last opinion, Messrs. Huxley and Hancock, two of the most eminent English naturalists, would place them among the Molluscoïda, by the side of the Ascidia and Bryozoa or Polyzoa.

This new mode of appreciating the affinities of this group led me to desire to study these creatures afresh; and when the opportunity was afforded me of investigating the faunas of great depths in the Mediterranean, I hastened to resume observations commenced about 1858 in the sea off Corsica.

To determine the affinities of the Brachiopoda I seek in their nervous system for the criterion that must guide me. It is to the characteristic organ of animality that I apply myself, because, as has been so admirably shown by Cuvier, it furnishes the characters of highest value; and I compare it on the one hand to that of the Lamellibranchiata, and on the other to that of the Bryozoa.

In the Lamellibranchiate Acephalan the plan of organization is simple. The organs are repeated symmetrically on each side of the median line. Thus we find three double nervous centres—one near the mouth, another in the foot, the third between the base of the foot and the anus, near the branchiæ. Moreover certain organs have an existence, a peculiar symmetry, and very precise relations with these different centres.

Upon the median line are the mouth, the foot, and the anus. At the base of the foot, between it and the anus, on each side, beyond the ganglia of the third or pallio-branchial group, open the two glandular bodies called the glands of Bojanus; lastly, to the right and left of the mouth there are two pairs of labial *vela*, which vary greatly in form in the different species.

To compare this well-known plan, which it was necessary to refer to here, with that of the Brachiopods, we must first of all place the animals in a comparable position. Suppose, for example, that we have a *Terebratula* and an *Anodonta* to compare: the former must be placed with its ligament downwards, its apophysary valve to the left of the observer, and its perforated valve to his right; the second must have its hinge to the left and its mouth upwards. Most figures show the Brachiopoda in a position the reverse of that just indicated, which renders their comparison with the Acephala more difficult.

In the animals thus placed the first difference that presents itself, and that which has most caught the attention of observers, is this: the *Anodonta* has its valves lateral; the *Terebratula* has one of them dorsal, the other abdominal.

This difference, which appears very great, has not quite so much importance as we should be inclined to attribute to it at first sight; we need only free it from the secondary conditions which surround it, so as to see only the fundamental parts. Thus the greatly developed and multiplied muscles have become longitudinal and symmetrical, in consequence of the arrangement of the valves, and they have attracted the attention of naturalists perhaps too specially, and led them to neglect other more important organs.

As the Brachiopod lives attached, a special locomotive organ would be useless to it; therefore its foot is aborted, and with it the corresponding portion of the nervous system. Here, morphologically speaking, we have a great and fundamental difference, very different from that presented by the position of the valves.

On each side of the mouth of the *Terebratula* we find two long fringed arms, rolled up in a spiral form, and accompanied by a membranous lip; these are the analogues of the labial vela of the Lamellibranchiata. The investigation of the nervous system justifies this notion; for there exist two small symmetrical ganglia which, with the assistance of the long commissure uniting them, surround the œsophagus like a collar, and furnish nerves to the arms, as in the Lamellibranchiata the analogous ganglia furnish the nerves to the labial vela.

These first ganglia, which are difficult to discover, correspond with the œsophageal ganglia of the other Mollusca; they are united by long connectives with the most highly developed and therefore most evident nervous masses, which are found above the mouth, in the median line, in the fold of the two lobes of the mantle. We know that this last organ performs, in great part, the function of the organ of respiration; and as it receives its nerves from this last ganglionic centre, this may be regarded as the analogue of the pallio-branchial centre.

As to the pedal ganglia, they do not exist, as the organ for which they are necessary is wanting.

The organs of Bojanus and those of reproduction open in the *Terebratula*, as in the *Anodonta*, symmetrically outside and by the side of the pallio-branchial nervous centre. Moreover, according to the beautiful investigations of Mr. Hancock, the heart in the Brachiopoda is dorsal, which furnishes an additional feature of resemblance between the two groups, for in this way the central organ of the circulation is separated from the organs of Bojanus and the pallio-branchial ganglia by the digestive tube.

Lastly, in the Brachiopod, as in the Lamellibranchiate Acephalan, the organs just referred to are repeated symmetrically on each side of the median line of the body.

Thus if we suppress in the Lamellibranchiate Acephalan the foot and the pedal ganglia, there remains an organism having the greatest

analogy with that of the Brachiopod, always excepting the position of the valves. Now this is also easy to be brought under the general plan of the *Anodonta*, if we suppose the two lateral lobes of the mantle to be united above the mouth and below the anus, and imagine that about the middle of its length an emargination is formed which may advance as far as the hinge; for then the two halves of the mantle are no longer lateral, but dorsal and abdominal, and the shell reproduces the pattern upon which it models itself.

The modifications undergone by the muscles are the consequences of the changes of arrangement which have taken place in the shell; they cannot invalidate the zoological approximation which I am endeavouring to establish. Do we not, for example, find an Ascidian (*Chevreulius*) presenting symmetrical muscles analogous to those of the Terebratulæ, and this merely because its tunic has become bivalve, and without one being able to remove it from the group to which it belongs?

If we now compare the Polyzoan or Bryozoan with the Brachiopod; we find some external resemblances, but profound differences of greater importance. No doubt the Bryozoan often presents an organ in the form of a horseshoe, placed close to the mouth, and which may be compared to the arms of the Brachiopods; but this is not a sufficient feature of resemblance to bring together animals so different. If we look at the nervous system, we shall soon be convinced.

Hitherto the Molluscoïda have presented only a very simple nervous ganglion, without an œsophageal collar, and without any very evident double symmetry; consequently they are more distant from the Brachiopoda than the latter from the Lamellibranchiata.

Thus the investigation of the nervous system legitimates the approximation which we are seeking to establish, and does not justify that which the English authors have attempted; but it leads us also to recognize the necessity of making a distinct group for the Brachiopods, which are much rather degraded Acephala than elevated Molluscoïda.

These zoological relationships are by no means invalidated by an organic peculiarity as curious as unexpected. Professor Huxley was the first to demonstrate the non-perforation of the anal extremity of the intestine in the Terebratulæ, and I have myself confirmed this observation in several other genera and species; this arrangement forms a very remarkable exception among the Mollusca, and appears to be especially proper to the Articulate Brachiopods, which really represent *Cœlenterate Mollusca*.

The preceding general observations constitute a *résumé* of minute and detailed investigations undertaken in 1858 in Corsica, and in 1862 in Algeria, upon the genera *Megerlia*, *Terebratulina*, *Thecidia*, *Argiope*, and *Crania*, which inhabit the Mediterranean, and were all observed living on the spots which they inhabit.—*Comptes Rendus*, November 6, 1865, pp. 800–803.